

Heat stress in captive endothermic animals

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Introduction

Approximately 26 billion captive animals, spanning over 10,000 species (Mason 2010) are housed in artificial habitats and face a wide range of potential environmental challenges. These include abiotic sources of stress, for instance, artificial lighting, exposure to loud or aversive sound, arousing odours and uncomfortable temperatures or substrates. In addition, confinement-specific stressors such as restricted movement, forced proximity to humans or conspecifics, reduced feeding opportunities and other behavioural restrictions (Morgan & Tromborg 2007). There is enormous variation between species in how they react to captivity, even among close taxonomic relatives (Mason 2010). Captive wild animals are often healthier, live longer and breed more successfully than conspecifics living free in their natural environments, due to the ample supply of food and water, veterinary care and protection from predation and conflict. However, this is not always the case; some captive wild animals survive and breed far less well than might be expected. Behaviour and Darwinian fitness have been shown to correlate to welfare (Jordan 2005); the evidence of compromised welfare of animals often suggests that physiological or psychological needs are not being met (Mason 2010).

Among the adaptive mechanisms that species possess to deal with various levels of environmental challenge, are a group of behavioural and physiological responses to stress. For the purpose of this review, Moberg's (2000) definition of 'stress' as 'the biological response elicited when an individual perceives a threat to its homeostasis' and 'stressor' as 'anything that challenges homeostasis' will be used. A 'stressor' in this case may be an actual physical challenge, or the threat of such a challenge. In either case, stressors result in an evolved cascade of physiological, hormonal and behavioural responses, termed the stress response (Romero 2004). Stress is not always bad, yet it can have a damaging effect on the individual. It is important to recognise stressors that adversely affect an animal's welfare. There is a 'biological cost of stress' because the changes in biological function during the stress response result in a shift of resources away from biological activities occurring before the stressor (Moberg 2000). During prolonged or severe stress, the individual will have insufficient biological reserves to satisfy the cost of the stress response. Resources must then be shifted away from other biological functions which become impaired and the animal experiences distress. The animal enters a pre-pathological state and becomes at risk of developing a pathology that can jeopardise health and survival (Nelson 2005). Prolonged sympatho-adrenal activation, corticosteroid

secretion and increased cardiac tone contribute to the development of cardiovascular disease. Inhibited reproductive function and myopathy are inevitable when glucocorticoid secretion is prolonged, and in severe cases the irreversible loss of heart muscle cells can occur. The stress induced elevation of blood glucose levels cannot continue indefinitely and prolonged inhibition of digestion results in gastric ulceration and chronic bowel distress syndrome. Suppressed immune function can lead to peptic ulcers because the proliferation of bacteria in the gastrointestinal tract can attack the stomach or duodenum lining. Chronic immunosuppression compromises long-term survival. Chronic stress also inhibits growth and repair processes

Captive animals often experience a different climate to that which they are adapted. In this review I first consider the various thermal regulatory adaptations that endothermic species possess. The focus then moves to the potential affect that heat stress has on captive animals, before reflecting on animal welfare and implications for management.

Thermoregulation in endotherms

Body temperatures vary universally within and among individuals. Among species of birds, mean body temperatures vary from 36 to 45°C and from 35 to 41°C during activity and rest, respectively (Prinzinger et al. 1991) and even more variation exists among species of mammals. The body temperature of an organism is a balance between the rate at which heat is supplied and the rate at which it is lost. For an endotherm the two sources of heat are metabolism and the environment. Losses occur through the skin, the rate of which is influenced strongly by external temperature and insulation, and also as a result of evaporation associated with respiration (Clarke & Rothery 2008). The main purpose of the thermoregulation system is maintaining temperature homeostasis in the thermoneutral zone (TNZ) (Ivanov 1999); the range of ambient temperatures over which the animal's metabolic rate or evaporative water loss is not varied (Blache et al. 2011). Animals use specific strategies to reduce, accentuate and control heat exchanges (Table 1). These can be considered under the general categories of avoidance and tolerance strategies and regulatory systems. Avoidance of environmental temperature extremes is an important part of the behavioural repertoire of numerous animals and is used as a first line of defence in many (Wilmer et al. 2005). Avoidance can be generally viewed as the location and use of appropriate climatic conditions in time and space. Nevertheless, many animals cannot continuously use avoidance strategies because at some point every individual has to feed, meet others of its species and reproduce; during these periods heat may be lost or gained from the environment or from metabolic effort supporting the activity, so that temperature regulation may need attention. Animals vary substantially in their tolerance of varying body temperatures, and thus in the temperatures that elicit acclimatory or regulatory responses. The thermal tolerance range is the full range of body temperatures over which an animal can survive indefinitely. A broader tolerance zone is the thermal survival zone which is between the upper critical temperature and the lower critical temperature (Wilmer et al. 2005).

Morphological adaptations illustrate the profound effect that thermoregulation has in terms of fitness and hence the evolution of advantageous anatomical structures (Louw 1993). An individual cannot change its morphology, so these adaptations may render a species more vulnerable to heat overload or excessive loss when in captivity.

Table 1: Endothermic regulatory strategies. Information from Louw (1993); Fish et al. 2002; Wilmer et al. 2005; Rajchard (2010).

	Behavioural	Physiological	Morphological
Heat production and maintenance	<ul style="list-style-type: none"> • Locating an appropriate microclimate • Evasion (torpor, hibernation, migration) • Voluntary muscular activity • Changing effective surface area • Group behaviours e.g. huddling 	<ul style="list-style-type: none"> • Involuntary muscular activity (shivering) • Nonshivering thermogenesis • Digestion provides a minor source of heat • Peripheral vasoconstriction and other blood shunting strategies • Decrease thermal conductance: piloerection or ptiloerection • Long term: growth of denser fur/feathers, deposition of thicker adipose layers 	<ul style="list-style-type: none"> • Counter-current heat exchangers in extremities • Colouration • Size and shape • Insulation • Underfur possessed by semi-aquatic mammals • Water resistant feathers due to oil gland secretion
Keeping cool	<ul style="list-style-type: none"> • Locating an appropriate microclimate • Evasion (torpor, aestivation) • Evaporative cooling: wetting or spreading saliva over surface • Changing effective surface area 	<ul style="list-style-type: none"> • Peripheral vasodilation and other blood shunting strategies • Flattening of fur or plumage • Partial raising of fur or plumage when air temperature exceeds body temperature • Evaporative cooling through sweating or panting – usually a ‘last resort’ strategy; animals often lack the necessary water reserves 	<ul style="list-style-type: none"> • Transient hyperthermia (heat storage) • Heat exchange systems in some species prevent the brain overheating • Peripheral heat exchange systems can become temporary thermal windows for heat dissipation • Colouration • Size and shape • Insulation

Heat stress in captivity

Zoos tend to keep certain popular species regardless of their location (International Species Information System, ISIS). In captivity individuals are routinely exposed to temperatures for which their species is not morphologically or physiologically adapted and the ability for animals to thermoregulate by behavioural means can be greatly reduced or absent altogether (Morgan & Tromborg 2007). The consequences for animals under these conditions are often far from ideal. Extreme temperatures are well-known stressors, and indeed are used as provocateurs in studies of behavioural and physiological responses to stress. It is not surprising therefore, to find temperature as a common source of discomfort

and distress in captive animals. Polar and sub-polar species such as the polar bear (*Ursus maritimus*), arctic fox (*Vulpes lagopus*), leopard seal (*Hydrurga leptonyx*), macaroni penguin (*Eudyptes chrysolophus*) and arctic tern (*Sterna paradisaea*) are maintained in captivity all over the world (ISIS), in temperatures far higher than in their natural environment.

Thermal physiologists commonly use the term 'heat stress' to mean the demand made by the environment for heat dissipation (Silanikove 2000). Heat stress may be of greater concern than cold stress because the 'safety margin' between normal core temperature and lethal hyperthermia is smaller than that for lethal hypothermia (Blache et al. 2011). Hyperthermia may damage every organ in the body, but the central nervous system (CNS) and reproductive systems are the most sensitive (Fowler 1996). Impaired mental function, convulsions and coma are signs that heat stress is having a marked effect on the brain, whilst reduced birth weight, foetal damage, birth defects and abortion are profound effects of heat stress during pregnancy. In males, excessive heat kills sperm. Other pathological effects of stress in general were mentioned above.

Behaviour alteration is usually the first response to an increased heat load. Avoidance of the extreme temperature, by locating a more suitable microclimate, is a typical response. Stoinski et al. (2002) conducted a postoccupancy evaluation on four naturalistic western lowland gorilla (*Gorilla g. gorilla*) enclosures at Zoo Atlanta. A linear trend toward decreasing visibility with increasing temperatures was found. There appears to be an increased attraction to buildings in warm temperatures because they provide excellent shade, are located next to a cool concrete substrate and hold a water source. The buildings are primarily in nonvisible parts of the exhibits, resulting in decreased visibility on warm days. Brent et al. (2003) provide evidence for significant behavioural changes related to ambient temperature in outdoor-housed captive mother-infant baboons (*Papio hamadryas anubis* sp.). Thermoregulatory needs differ between adult and infant baboons due to their difference in size; therefore ambient temperature is likely to generate mother-infant conflict. The mother's behaviour was more affected by temperature than the infant's, indicating that thermoregulation requires more behavioural adjustments for the mother baboon. The frequency of the mother making and breaking contact was higher during hotter temperatures. Ventral contact and huddling was significantly negatively correlated with temperature. The data suggests that the rate of contact between mothers and infants may have as much to do with maintenance of body temperature as with other behavioural or nutritional needs. However, these findings are at odds with the results of a study by Schino and Troisi (1998) who report that temperature does not significantly impact the amount of ventral contact between mother and infant Japanese Macaques (*Macaca fuscata*). Clearly, the influence of climate on mother-infant behaviour in nonhuman primates requires more study.

When behavioural strategies fail to maintain body temperature, heat stress can elicit a physiological response. Scholander et al. (1950) established that large arctic species, such as eskimo dogs (*Canis lupus familiaris*), arctic foxes (*Vulpes lagopus*) and glaucous gulls (*Larus hyperboreus*), have a broad zone of thermoneutrality, from +30°C to -40°C, which shows their ability to change heat dissipation by a factor of 11, even when lying down. Vasomotor control of the poorly insulated legs may play an important role in the general thermoregulation of these animals. Ass-Hansen et al. (2000) exposed Norwegian reindeer (*Rangifer tarandus tarandus*) to air temperatures which increased heat load. In resting, winter-adapted reindeer, the rate of respiratory heat loss is enhanced through thermal panting, at ambient temperatures above 0°C (Blix & Johnsen 1983). When exposed to mild heat loads, resting reindeer pant only through their nose (closed-mouth panting), whereas

when exposed to more pronounced heat loads, the animals alternate between periods of closed- and open-mouth panting (Johnsen et al. 1987). A steadily increasing heat load will impose a demand for enhanced respiratory evaporation. To further increase ventilation the animal shifts to open-mouth panting to allow the air to follow an alternative low-resistance route (Aas-Hansen et al. 2000). Norwegian reindeer are kept in Whipsnade Zoo, where the July daily mean temperature is 22.5°C (Met Office), so it might be expected that these animals suffer from heat stress. However, Muller et al. (2010) found that captive reindeer had life expectancies equal to or longer than free-ranging individuals, suggesting that reindeer perform well under human care. They propose that mean life expectancy of captive populations relative to that of corresponding free-ranging populations is a reliable indicator to evaluate the husbandry success of a species in captivity. However, lifetime reproductive success is our best estimate of biological fitness (Broom 1991); this can be compromised by a number of factors, not only longevity. Moreover, an individual may survive beyond its expected life time in captivity despite having poor welfare, for example, an impaired immune system, resulting from too frequent high activity of the adrenal cortex. Although adrenal activity can occur during beneficial activities, it generally indicates that the animal is having some difficulty in trying to cope.

Penguins are a popular exhibit in any zoo. In the past, hundreds of these birds, primarily Humboldt penguins (*Spheniscus humboldti*) were imported into the United States, where only a minute percentage survived in captivity (Davis 1967). Thankfully, since 1983 when the species was listed as threatened, no Humboldt penguin has been legally imported from the wild (Blay & Côté 2001). The penguin deaths which took place in the US (Davis 1967) generally occurred despite the zoos best efforts to preserve them. In 1978, Austin reported an alarming mortality rate of penguins at Detroit Zoo, where life expectancy rarely exceeded 90 days and reproduction was non-existent. Yet, Humboldt penguins have survived under extremely bad conditions. They have thrived in simple outdoor exhibits in Miami and Los Angeles where temperatures reach over 37.8°C (Davis 1967). Nevertheless, heat exhaustion is a key contributor to premature penguin death, during transit, immediately after arrival at the zoo and during extremely hot weather. Heat cannot be readily eliminated from the body due to the thick, dense feather layers, so subjecting the birds to an appreciable temperature increase will result in heat exhaustion and its accompanying syndrome of hypoxemia, hyperventilation, haemorrhage and dyspnea (Davis 1967). In 2005, The Association of Zoos and Aquariums (AZA) Penguin Taxon Advisory Group produced the third edition of a penguin husbandry manual. They provide optimum air temperature ranges for a number of species. For Emperor (*Aptenodytes forsteri*) and Adelie (*Pygoscelis adeliae*) penguins the absolute recommended upper temperature limit is -1°C. In 1987 Todd reported that traditionally most Emperors reaching captivity perished in the first year. Emperor penguins are extremely specialised and are totally restricted to the high Antarctic. It is now known that specialised facilities and life-support systems are required for maintenance and propagation of this species. *Spheniscus* penguins can be housed indoors or outdoors, although the success of an outdoor exhibit depends on the ambient temperature and relative humidity. Where the temperature rises above 29.4°C, provisions should be made to allow the birds a means of heat relief.

Animal Welfare

Welfare is a characteristic of an animal that should be measured in a scientific way that is free from moral considerations (Broom and Johnson 1993). Therefore welfare measurements should be based on: (i) environmental indices of heat stress, (ii) the animal's response in coping with difficulties, and (iii) on signs that coping effects to maintain homeothermy are failing.

The subdivision of the thermoneutral zone into a zone of thermal well-being is suitable to describe the relation between an animal and its environment from the viewpoint of animal welfare (Silanikove 2000). The marked effects of increasing heat stress and diminished welfare can be categorised into four stages:

- *Zone of thermal comfort*: energetic and physiological efforts of thermoregulation are minimal, health is optimum.
- *Stage 1 (the innocuous stage)*: heat stress activates strain responses (sweating, modest panting). Homeothermy is attained without difficulty, fitness is not hampered.
- *Stage 2 (the aversive stage)*: evaporative cooling mechanisms are intensified exponentially; water consumption must increase as a result. The animal is much more vulnerable to other environmental stressors.
- *Stage 3 (the noxious stage)*: two physiological responses are possible,
 - Feed consumption and thermogenic hormone secretion decrease to lower the basal metabolism, resulting in a reduction of the internal heat load. Reduced feed intake can be reflected in reduced productivity.
 - If an animal does not have an opportunity for adaptation, or with temperature rising further in adapted animals, cooling is insufficient to maintain homeothermy; body temperature rises.
- *Stage 4 (the extreme stage)*: animal enters into an acute phase of heat stress that induces heavy panting and maximal sweating. If these measures fail to stop the elevation of body temperature, a vicious circle sets in and the animal succumbs to heat stroke and dies. External emergency aid is needed to save the animal from immediate death.

Knowledge is severely restricted for most species living in captivity, yet it is often possible to draw on results from research involving livestock. It is well known that heat stress impairs livestock growth, milk production and reproduction (Silanikove 2000); an indication of poor welfare (Broom & Johnson 1993). Yet, no clear criteria exist as to conditions in which heat stress relief is needed. Ambient temperature, solar radiation, wind speed and humidity are the main environmental stressing factors for an animal in a hot climate (Silankove 2000). The temperature humidity index (THI) is useful for assessing thermal stress (Berman 2005). THI values for Holstein cows of <70 are considered comfortable, 75-78 stressful, and values >78 cause extreme distress and animals are unable to maintain thermoregulatory mechanisms or normal body temperature (McDowell 1976). However effects such as air velocity, radiation, and factors such as the posture and density of animals, their heat production, and coat insulation are not accounted for in the THI. The complex interactions between factors that govern heat exchange make it almost impossible to use a simple physical measurement of the environment as a satisfactory index of thermal stress, and hence welfare. In addition, the impact of the environment may be modified by animal behaviour and can differ on a species, breed and individual level. The susceptibility to other stresses may exacerbate the effects of heat stress, emphasising further the problematic nature of establishing a useful relationship between heat stress indices and animal welfare (Silankove 2000). However, there has been some success with thermal balance models, which consist of animal specific data (body weight, metabolic heat production, tissue and coat insulation, skin water loss, coat depth and minimal and maximal tide volumes) and of general heat exchange equations. A thermal balance simulation model was modified to adapt it for Holstein cows (Berman 2005). Environmental conditions at which respiratory heat loss attained approximately 50% of its maximal value were defined as thresholds for intermediate heat stress. A large variation in thresholds due to

environmental and animal factors was found. Using such models may make it possible to estimate threshold temperatures at which heat stress relief is required for a wide range of species and environmental situations.

Rectal temperature is generally considered a good index of deep body temperature even though there is considerable variation at different parts of the deep core at different times of the day (Srikandakumar et al. 2003; Srikandakumar & Johnson 2004). McCrabb et al (1993a,b) found that ewes of the same flock and breed that maintained a lower rectal temperature (<39.8°C) produced lambs with higher birth weight than sheep with higher rectal temperature (>39.8°C). McCrabb et al (1995) later concluded that measurement of rectal temperature in sheep exposed to a hot environment in any one year is an accurate index of their rectal temperatures during subsequent years. Although measuring rectal temperature is a good physiological parameter to objectively monitor welfare, it is not always practical. Measuring the respiration rate would be a relatively easy way of identifying whether an animal has entered into one of the stages mentioned above, but basal rate data is not available for many species.

Establishments keeping animals in captivity must abide by legislation concerning animal welfare. Secretary of State's Standards of Modern Zoo Practice (SSSMZP), state that *'the temperature of enclosures must be suitable for the comfort and well-being of the particular species of animal at all times.'* Captive management husbandry manuals are available to provide guidance for a particular species, such as the penguin husbandry manual mentioned above. AZA also provide several completed animal care manuals (ACMs). The goal of the ACMs is to facilitate the development of consistent animal care practices across taxa for the wide variety of species regularly held in zoos and aquaria (Butterworth et al. 2011). In addition to ACMs, the AZA Accreditation Standards (AZA 2011) are intended to set the stage for good welfare at the species level; only those zoos and aquariums that meet the high standards receive accreditation. Brookfield Zoo is instituting a zoo-wide program of keeper-based behavioural observation, with the goal of establishing and maintaining a baseline of 'normal' or typical behaviour for individual animals which serves as a basis for comparison when social or environmental changes are implemented. This should provide an early indication of impending medical or welfare issues (Margulis & Walsh 2001). The continual monitoring of animals by trained and experienced staff would enable deviations in behaviour to be recognised. With this in mind, it would be possible to implement strategies to provide heat relief before they even become necessary.

Conclusion

Stress can have a damaging effect on an individual, and hence diminish welfare. If the stress is severe or prolonged, the biological cost can be significant, resulting in other biological functions becoming impaired. A range of behavioural and physiological responses can be elicited when heat load is increased. Popular species tend to be kept in zoos regardless of their location therefore it is imperative that heat stress can be recognised and some form of relief is provided. Research on livestock animals can provide us with an indication of thermal conditions required, but knowledge of the thousands of species kept in captivity is severely limited. A great deal more work therefore needs to be done on the specific needs of these captive species.

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